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Exploring body injuries in the horseshoe whip snake, *Hemorrhois hippocrepis*

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Abstract. Body injuries on snakes may serve as indices of predation rate, which is otherwise difficult to record by direct methods because of the usual scarcity and shy nature of these reptiles. We studied the incidence of body scarring and tail breakage in a Mediterranean colubrid, *Hemorrhois hippocrepis*, from south-eastern Spain. This species exhibits two traits that favour tail breakage, a long tail and active foraging tactics. The large sample (n = 328) of individuals acquired also enabled us to determine how the incidence of these injuries varies ontogenetically, between the sexes, in relation to energy stores, and to seek for the possible existence of multiple tail breakage. Overall, the incidence of tail breakage was rather low (13.1%) and similar to that of body scarring (12.7%). However, there was a significant ontogenetic shift in the incidence of tail breakage; such injuries barely appeared in immature snakes but stub-tailed individuals were present in 38.7% of snakes in the upper decile of body size. In contrast to most other studies, our data show a sex difference in the incidence of these injuries, adult male rates quadrupling those of adult females for body scarring and males maintaining larger stubs, probably because of the presence of copulatory organs housed in the base of the tail. Larger individuals did not have shorter tail stubs, a finding that does not support the multiple-tail-breakage hypothesis. Our results also fail to support the idea of a cost of tail breakage or body scarring in terms of body condition.

Keywords. Body scarring, predator-prey relationship, Spain, tail breakage

INTRODUCTION

In snakes, direct evidence of predator-prey interactions is difficult to obtain under natural conditions, because of their secretive behaviour (Willis et al., 1982; Gregory, 2016). Many species, however, exhibit tail breakage, a defence that favours escape from predators (Arnold, 1988; Greene, 1988) and that can be used as indirect evidence of the rate of predation (Pianka, 1970; Martins, 1996). When grasped by the tail, after thrashing vigorously and rotating the body longitudinally in one direction, some snakes undergo an intervertebral tail breakage (Greene, 1988; Todd and Wassersug, 2010). In contrast to typical saurians, the tail of snakes is not regenerated following breakage (pseudoautotomy; Savage and Slowinski, 1996), leaving a permanent record of the event. A possible drawback of this way of assessing predation pressure in snakes is that tail breakage could simply indicate inefficient predation, because the prey survives (Schoener, 1979; Medel et al., 1988; Mushinsky and Miller, 1993). However, some studies have found that snakes from study sites with fewer predators show a much lower frequency of tail breakage than did those from sites with far more predators (Placyk and Burghardt, 2005; Santos et al., 2011). Nonetheless, ecological factors other than predator pressure might influence the frequency of body injuries (Placyk and Burghardt, 2005); for example, tail breakage may also result both from encounters with dangerous prey (Gregory and Issac, 2005), a possibility that can be assessed only in study

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areas lacking snake predators (e.g., in Pantelleria Island; Cattaneo, 2015), as well as from incomplete skin sloughing and parasitism (Degenhardt and Degenhardt, 1965; Harkewicz, 2002).

Other body injuries of snakes, such as body scarring, might also indicate the rate of predatory attacks, although body scarring mostly reflects the efficiency of such attacks (Placyk and Burghardt, 2005; Sparkman et al., 2013); that is, inefficient predators tend to inflict injuries upon their prey, but the prey tend to survive, and the opposite for efficient predators (Seligmann et al., 1996).

In recent decades interest has increased in analysing the rate of body damage in snakes and has provided evidence of ontogenetic and sexual variation in body damage (Mendelson, 1992; Fitch, 2003), correlations between injury rates and life-history traits (Pleguezuelos et al., 2007), habitat-related differences (Akani et al., 2002), differences in predation pressure among populations (Santos et al., 2011), geographic distribution of injuries (Dourado et al., 2013), and the cost of such injuries (Pleguezuelos et al., 2013).

The horseshoe whip snake, *Hemorrhois hippocrepis*, a medium to large-sized colubrid distributed throughout the Western Mediterranean Basin, exhibits two traits that favour the appearance of body damage, particularly through tail breakage: (1) it is an active forager and (2) is long tailed (Pleguezuelos and Feriche, 2014). In animals, foraging mode (active vs sit-and-wait; Schoener, 1971) influences other natural history traits of the species, such as predation pressure (Webb et al., 2003). Active foraging strategies normally imply high rates of exposure to potential predators. That is, while the forager actively searches for food, it increases the risk of predation from other predators (Huey and Pianka, 1981; Secor, 1995), and even of injuries from prey (Greene, 1997). With respect to the second trait, tail breakage is known to have a higher incidence in long-tailed snakes (Willis et al., 1982; Mendelson, 1992; Bowen, 2004), including *H. hippocrepis* (Marco, 2002).

We examined the frequency of tail breakage and body scarring in *H. hippocrepis* from the south-eastern Iberian Peninsula. The large sample of specimens also enabled us to test several hypotheses about patterns of injury acquisition:

1. The tail-breakage/body-scarring hypothesis, which predicts that fewer specimens will have scars on the body than will show damaged tails, as a consequence of attacks to the body being more lethal than attacks to the tail resulting in tail breakage (Placyk and Burghardt, 2005).
2. The size-related hypothesis, which predicts that the frequency of body injuries in snakes should be higher in larger and presumably older individuals, because they have been exposed to potential predators for a longer time than smaller ones have (Seligmann et al., 2008; Pleguezuelos et al., 2010).
3. The sex-related hypothesis has a dichotomy: i) some authors predict that the frequency of tail breakage or body scarring in snakes will be higher in males, because individuals of this sex move greater distances during the mating period than do females, being more exposed to potential predator attacks (Vitt et al., 1974), and indeed, many more adult males than adult females have been recorded for this species in the study area during the mating season (Pleguezuelos and Feriche, 2014); ii) other studies have reported lower frequencies of tail breakage in males (Willis et al., 1982; Mendelson, 1992; Placyk and Burgahardt, 2005), which has been explained by the higher mortality and the decrease in reproductive success of the stub-tailed individuals of this sex (Shine et al., 1999). We will consider also the effect of sexual dimorphism in body size in the appearance of sexual differences in tail breakage.
4. The multiple-breakage hypothesis predicts that the stumps of damaged tails will be shorter in larger and presumably older individuals than in smaller ones, as a consequence of snakes suffering multiple breakage events over life (Savage and Crother, 1989; Slowinski and Savage, 1995).
5. The cost-of-injuries hypothesis, which predicts that despite the immediate advantage of tail breakage or body scarring for the survival of the individuals, these wounds also imply negative consequences. The costs would derive from impaired locomotion (Martin and Avery, 1998), and consequent decreased foraging ability, reproductive output or survival (Wilson, 1992; Downes and Shine, 2001; Maginnis, 2006). The cost-of-injuries hypothesis predicts that damaged individuals are smaller (because they survive for a shorter time) and have lower body condition than undamaged ones would (Pleguezuelos et al., 2013).

MATERIAL AND METHODS

Study area

We examined specimens of *H. hippocrepis* from an area of approximately 20 000 km^2 in the south-eastern Iberian Peninsula (coordinates 37°15'-38°45'N; 2°30'-5°45'W); all specimens were from altitudes between 0-1100 m a.s.l. Mean annual temperature averaged 16.4ºC, and the average yearly rainfall was 412.1 mm (data summarized in Moreno-Rueda et al., 2009). The landscape is dominated by cultivation (olive orchards, cereal crops), mixed areas of evergreen forest and scrubland

(*Quercus ilex*), and pine plantations (*Pinus* sp.). Within the study area, *H. hippocrepis* is preyed upon by three reptiles, four diurnal raptors and one mammal species (Pleguezuelos and Feriche, 2014), and predator composition is rather consistent.

Data on morphology and body condition

The data (n = 328) came from vouchers in the collection of the University of Granada (Spain), collected from 1985-2015 as road kills or killed by local people. We measured snout-vent length (SVL ± 1 mm) of all specimens, as well as the number of subcaudal scale pairs (SBC) in tail-damaged specimens. Adult individuals were sexed by dissection. We checked for tail completeness and classified individuals as tail damaged or tail undamaged. This classification was conservative, as we considered the tail to be damaged only in individuals with a healed tip of the tail. Non-predatory agents, such as incomplete skin sloughing (Harkewicz, 2002), can also lead to tail loss. To minimize bias derived from these circumstances, individuals with just the apical scale missing were not considered cases of tail breakage. We also checked all individuals for the presence of body scars, again conservatively, ignoring road-killed specimens that were badly damaged (i.e., with body parts that could not be evaluated for body scarring; Fitch, 2003).

To analyse if our results were confounded by the provenance of most samples (road-kills), we compared the prevalence of body injuries in our data set with a small sample of animals captured alive in the same study area from 2005-2015 and released at the capture site after measurements.

We tested the tail-breakage/body-scarring hypothesis for adult individuals only by comparing the frequency of those characters between groups (by a contingency table; individuals with damaged tail and those with body scarring). If this hypothesis is true, there will be more individuals with tail damaged than with body scars.

The hypothesis of ontogenetic shift in tail breakage was assessed following the procedure in Pleguezuelos et al. (2010). We divided body size into 10 classes of equal numbers (n = 31) and fitted the best function (among linear, exponential and polynomial, according to the r coefficient) to the relationship between frequency of tail breakage with body size (medians of each body size class). If this hypothesis is true, the rate of tail breakage will be higher in the classes of the largest (because probably older) individuals.

We tested the sexual hypothesis by comparing (by a contingency table) the frequency of adult males and females (males SVL > 540 mm, females SVL > 680 mm; Pleguezuelos and Feriche, 2014) with damaged tails and body scarring. If this hypothesis is true, it would be sexual differences in the frequency of body injuries.

We tested the multiple-tail-breakage hypothesis by correlation of the number of remaining SBC on SVL, the latter trait acting as a crude surrogate for age, using only the subsample of snakes with damaged tail (Mendelson, 1992); if this hypothesis is true, the number of SBC should diminish with SVL of the individuals. Because of the minor sexual dimorphism in the SBC scales (Feriche et al., 1993), we pooled the two sexes.

We tested the body-condition hypothesis by comparing fat-body level in injured vs. non-injured individuals (by the Mann-Whitney U test). In snakes, body condition is strongly influenced by fat-body reserve (Bonnet et al., 2003), and body condition of our sample was estimated according to the importance of fat bodies (Waye and Mason, 2008). We were unable to accurately weigh some road-killed specimens or their fat bodies, so we scored fat reserves of *H. hippocrepis* into five visual categories, from 0-4 (description of the procedure in Pleguezuelos and Feriche, 1999). Because the fat-body reserves in this species exhibit ontogenetic, sexual, and seasonal shifts (Pleguezuelos and Feriche, 1999), we excluded immature individuals from this analysis, thereby removing most of the ontogenetic effect, and then considered the two sexes separately. However, we were unable to account for the seasonal effect on fat-body level (because of sample size), although most of the individuals of the sample came from spring. If this hypothesis is true, injured individuals will exhibit worst body condition than non-injured ones.

Distributions of data were checked for normality prior to analyses; mean values are followed by ± one SD with alpha set at 0.05. The statistical analyses were performed using STATISTICA 7.0.

RESULTS

We analysed 126 adult males, 104 adult females, and 98 immature or of undetermined sex of *H. hippocrepis*. The sample size for the different traits considered here varied, because of the varied preservation status of the vouchers.

The tail breakage and body scarring hypothesis

Across the study area, 13.1% of *H. hippocrepis* voucher individuals had damaged tails (n = 328) and 12.7% had scars (n = 180), mostly in the body (n = 16) and a few on the tail (n = 5), with only one on the head. Only eight individuals shared both injuries, tail breakage and body scars. There was no difference in the frequency of individuals with tail breakage and body scarring (2 × 2 table, $\chi^2 = 0.36$, P = 0.54). The small sample of live individuals exhibited approximately the same prevalence of tail breakage (12.5%, n = 32; $\chi^2 = 2.35$, P = 0.12) and body scarring (8.3%, n = 24; not compared statistically because of small sample size) as the sample of road-kill snakes.

The size-related hypothesis

Stub-tailed snakes were larger than those without tail breakage (x ± SD = 880.6 ± 268.6 mm, n = 42 vs. 606.8 ±

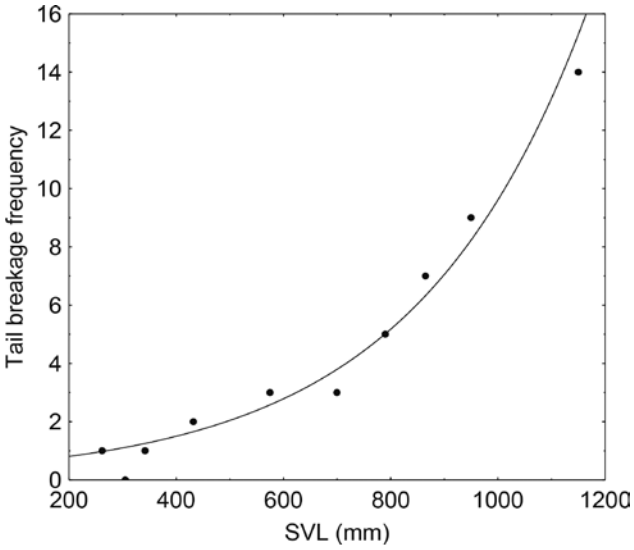

Fig. 1. Fit of tail-breakage frequency (number of snakes in each size class with tail breakage) to medians of 10 custom body-size classes (snout-vent length) in *Hemorrhois hippocrepis* from SE Iberian Peninsula (n = 310). The criterion for the limits of the body-size classes was to have the same sample size (n = 31). The solid line represents the quadratic function estimated ($y = 0.000018x^2 - 0.0034x + 0.547$; $r^2 = 0.972$, $P << 0.001$).

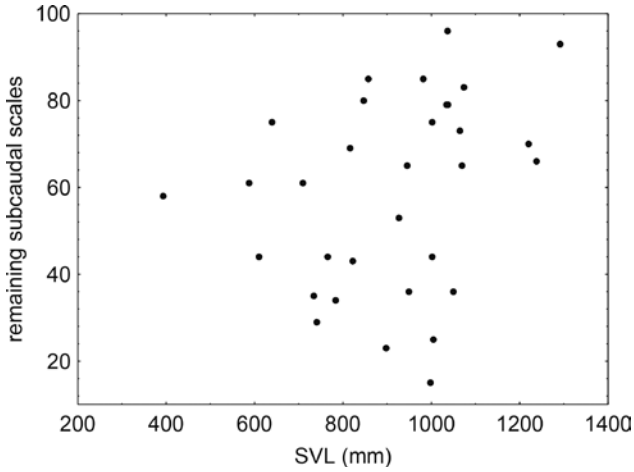

Fig. 2. Relation of subcaudal scale pairs to body size (snout-vent length) in *Hemorrhois hippocrepis* from SE Iberian Peninsula affected by tail breakage.

222.9 mm, n = 266; t = 6.269, P << 0.001, test of homogeneity of variances, P = 0.149), and this result held true when the sexes were considered separately (t test, 123 males and 102 females, P = 0.01 in both comparisons). Individuals with body scars were larger than unscarred specimens (x ± SD = 1005.1 ± 128.1 mm, n = 22 vs. 746.3 ± 217.9 mm, n = 162; M-W U test, Z = 5.23, P << 0.001), results that again held when the sexes were considered separately (M-W U test, 95 males and 69 females, P = 0.05 in both comparisons). Moreover, the frequency of tail breakage increased according a quadratic function with increasing body size; fewer than 5% of snakes in immature size classes exhibited tail breakage, and 38.7% of snakes in the body class of largest snakes (1005-1292 mm SVL) exhibited tail breakage (Fig. 1). Because of small sample size, this analysis was not executed for the individuals with body scars.

The sex hypothesis

There was a difference between the sexes in body injuries only for body scarring: 20.9% of the males (n = 86) and 4.7% of the females (n = 63; 2 × 2 table, χ^2 [Yates corrected] = 4.95, P = 0.02) exhibited body scarring, and 27.3% of the males (n = 99) and 16.2% of the females (n = 74; 2 × 2 table, $\chi^2 = 1.90$, P = 0.16) exhibited tail breakage. Moreover, there was a sexual difference in the number of SBC scales remaining in the stub of damaged tails: males had more SBC pairs (x ± SD = 63.9 ± 20.6, n = 22) and hence had a longer tail, on average, in broken tails than did females (x ± SD = 44.9 ± 22.3, n = 11; t = 2.43, P = 0.05; test of homogeneity of variances, P = 0.72). The mean number of SBC in males and females with intact tails proved very similar (Feriche et al., 1993).

The multiple-tail-breakage hypothesis

Tails of *H. hippocrepis* can break over almost their entire length, as we found broken tails with between 15-96 pairs of remaining SBC scales (mean number of SBC scales for individuals with intact tails from the study area, 102.8; Pleguezuelos and Feriche, 2014). The number of SBC scales remaining on stub-tailed individuals did not differ according to body size, whether sexes were combined (r = 0.283, n = 47, P = 0.115; Fig. 2) or considered separately (males, r = 0.413, n = 22, P = 0.06; females, r = -0.386, n = 10, P = 0.27). Thus, larger individuals did not have shorter tail stumps than smaller individuals, a finding that does not support the multiple-tail-breakage hypothesis.

The cost-of-injuries hypothesis

Fat-body level did not differ between stub-tailed and whole-tailed snakes (x ± SD = 2.46 ± 1.26, n = 28 vs. 2.29 ± 1.26, n = 153; M-W U test, $Z = 0.572$, $P = 0.56$), and this result held when the sexes were considered sepa-

rately (M-W U test, 86 males and 72 females, P = 0.79 in both comparisons). Fat-body level did not differ between snakes with body scars and those without scars (x ± SD = 2.70 ± 1.26, n = 17, vs 2.53 ± 1.18, n = 100; M-W U test, Z = 0.605, P = 0.54); because of small sample size, separate analyses were not performed for each sex. These results for *H. hippocrepis* fail to support a cost of tail-breakage or body-scarring in terms of body condition.

DISCUSSION

General analysis and the relationship between trail breakage and body scarring

When a snake moves widely, it increases its risk of predation (Huey and Pianka, 1981; Secor, 1995). *Hemorrhois hippocrepis* is an active forager (Pleguezuelos and Feriche, 2014) and thus would be expected to undergo high predation risk and a high rate of body injuries (Mushinsky and Miller, 1993). However, the rate of tail breakage that we observed is rather low compared with other snakes (see Mendelson, 1992; Aubret et al., 2005; Gregory and Isaac, 2005; Pleguezuelos et al., 2010; Dourado et al., 2013, and references therein). We interpret the low rate of body injuries as reflecting the habits of this species, i.e., being a fast-moving snake that frequently dwells in vertical habitats (rocky slopes), traits propitious for escaping from predators. Consistent with this, *H. hippocrepis* has been recorded in only 8.7% of the pellets of the main snake-eater in the study area, the short-toed eagle, *Circaetus gallicus*, whereas another colubrid of similar size and foraging habits but slow moving, *Rhinechis scalaris*, was present in 39.5% of the pellets (Gil-Sánchez and Pleguezuelos, 2001). In Pantelleria Island (Sicily Channel), Cattaneo (2015) reported a very high incidence of tail breakage (55.6%, n = 34) for the (probably introduced) population of *H. hippocrepis*. However, this result was influenced by the large body size of individuals in the sample (see below); furthermore, injuries apparently were not caused by predators, but by prey, as the adults of this snake population rely mainly on a large and dangerous prey, *Rattus rattus* (Cattaneo, 2015).

Efficient predators more often kill their prey than injure them, whereas inefficient predators cause numerous injuries and fewer deaths (Stephens and Krebs, 1986; Seligmann et al., 1996). Predatory attacks to the snake's body or head may be more successful than those directed at the tail, and thus more individuals should be found with damaged tails than with body scars (Stephens and Krebs, 1986; Placyk and Burghardt, 2005). Although in absolute terms, we found a similar frequency of the two injuries in *H. hippocrepis* when we took into account that the head plus the body represents more than 75% of the total length of this species (i.e., the tail accounts for less than 25% of the total length; Feriche et al., 1993), our results support the tail-breakage/body-scarring hypothesis. Despite the small fraction of total length that the tail represents, approximately the same number of individuals exhibited injuries in the tail as along the rest of the body. This result suggests that *H. hippocrepis* survives tail attacks better than body grasping by predators. In snakes, scarring frequency may be a better indication of predator efficiency than predator intensity (Placyck and Burghardt, 2005).

The size-related hypothesis

This hypothesis has often been supported in snakes (White et al., 1982; Mendelson, 1992; Seligmann et al., 2008; Dourado et al., 2013). Mendelson (1992) proposed that larger snakes may be attacked and survive more frequently, and Willis et al. (1982) suggested that this result is the consequence of a survival cost of this trauma, because smaller and injured individuals were simply eliminated from the population. We propose that the struggling capacity of smaller snakes against predators is much weaker than in larger snakes, and that most encounters between predators and small snake individuals end in successful predation (Bittner, 2003; Pleguezuelos et al., 2010). However, larger *H. hippocrepis* would confront most of their predators with some bouts ending in body injuries but unsuccessful predation. In support of this, in our study area the snake-eater specialist, *C. gallicus*, does not consume snakes larger than 1190 mm SVL and scarcely those larger than 1000 mm SVL, presumably because the struggling capacities of larger snakes would be dangerous for the eagle (Gil-Sánchez and Pleguezuelos, 2001). However, this speculation needs confirmation by population studies. The most cautionary interpretation of the size-related hypothesis is that larger, and probably older, specimens were exposed to potential predators for a longer period and thus had an increased cumulative likelihood of injury (Schall and Pianka, 1980; Seligmann et al., 2008; Sparkman et al., 2013).

The sex hypothesis

In snakes, males usually move more than females in the mating period, and this sex difference in behaviour would expose males to greater predation pressure (Shine et al., 2001). In support of this hypothesis, we found that more adult males than adult females exhibit body scarring, in agreement with the sex differences in activity of *H. hippocrepis* as measured by the encounter rate in the

field. That is, during spring and particularly during the mating period of this species in the study area (May-June; Pleguezuelos and Feriche, 1999), the number of males recorded was more than two-fold that of females, whereas no difference was found over the rest of the year (based on 171 records; unpub. data of the authors). Male snakes searching for mates can also allow a much closer approach than snakes not seeking mates (Shine et al., 2003; Gregory, 2016). Moreover, this result must partially be the consequence of the sexual dimorphism in body size of *H. hippocrepis*; males, being larger than females (Pleguezuelos and Feriche, 2014), will exhibit higher frequency of body scarring (see the size-related hypothesis). Other authors have found more tail damage in females than in males (Willis et al., 1982; Slowinski and Savage, 1995), and have proposed that this was because females survive tail attacks more than males do (Placyck and Burghardt, 2005). However, neither our study nor others would be decisive in establishing the real existence of sex differences in predation pressure, and most studies of body injuries of snakes that have considered sex as a factor have failed to find differences between males and females (Zug et al., 1979; White et al., 1982; Mendelson, 1992; Mushinsky and Miller, 1993; Capula et al., 2000; Aubret et al., 2005; Pleguezuelos et al., 2010; Dourado et al., 2013).

Notably, *H. hippocrepis* males with tail breaks retain more pairs of SBC scales, namely a longer stub (see Dourado et al., 2013), than females. Mendelson (1992) observed the same in *Coniophanes fissidens* and related this finding to the copulatory organs housed in the base of the male's tail; breakage affecting the hemipenis or retractor muscles would be more harmful than breaks that leave longer tail stubs (Placyck and Burghardt, 2005). This could explain the low frequency of males with very short tail stubs.

The multiple-tail-breakage hypothesis

Evidence supporting this hypothesis has been obtained only in snake species with long tails that survive repeated attacks and injuries (Henderson, 1984; Savage and Crother, 1989; Savage and Slowinski, 1996). Without breakage, *H. hippocrepis* exhibit a rather long tail (see above), as is usual in snakes with strong climbing abilities (Pizzatto et al., 2007). However, we failed to support this hypothesis for *H. hippocrepis*.

The cost-of-injuries hypothesis

In some reptiles a cost of body injuries has been observed in terms of a reduction in feeding efficiency (Dial and Fitzpatrick, 1981). In *Thamnophis sirtalis*, Shine et al. (1999) found differences in body size and body condition of individuals depending on tail integrity. Thus, one deleterious effect of tail breakage or body scarring in *H. hippocrepis* could be a slower growth rate, preventing injured individuals from reaching the maximum body size within the population. However, we did not find smaller body size for injured individuals, but rather the opposite (see the size-related hypothesis). We also failed to find any difference in fat-body reserves between full-tailed and stub-tailed *H. hippocrepis*, suggesting than tail breakage did not affect foraging success in this snake, the same than in another snakes (Downes and Shine, 2001; Aubret et al., 2005; Maginnis, 2006; Pleguezuelos et al., 2013). The usually small portion of the tail lost in *H. hippocrepis* presumably did not affect mobility or foraging success, even in this climbing snake. Jayne and Bennet (1989) found that an ablation of at least two thirds of the tail was necessary to decrease locomotion speed by only 4.5% in *T. sirtalis*. Although there are no empirical data, the same must apply to body scarring.

We conclude that the analysis of body injuries in snakes can reveal and generate hypotheses on some aspects of their natural history, otherwise difficult to discover for these rather clandestine reptiles. Studying tail breakage and body scarring in *H. hippocrepis*, we have learnt that large individuals accumulate signs of inefficient predator attacks over their life, that males exhibit more body scars and longer stub-tails than females, and that the injuries considered here have no obvious cost for individuals bearing them. We admit that the sample for this study was gathered from a rather wide area and during a rather extensive period. However, there is no alternative way to obtain a large sample for some Mediterranean and terrestrial snakes, because of their scarcity and/or shy nature. In support of our procedure, in the same study area and during a shorter period, we found approximately the same percentage of live individuals of *H. hippocrepis* affected by tail breakage and body scarring; thus, there is no obvious bias in our sampling procedure. We encourage further studies on snake tail breakage and scarring, particularly studies based on large samples that can address the population-level consequences of injury (Gregory, 2016).

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